

Notes on the distribution of *Nepenthes* Species in Singapore

by

SALLY GREEN.*

Species found in Singapore.

N. gracilis Korth, *N. rafflesiana* Jack and *N. ampullaria* Jack are all common; *N. hookeriana* Lindl. and *N. trichocarpa* Miq. both occur rarely and singly. In the past *N. reinwardtiana* Miq. and *N. phyllamphora* Willd. were recorded from the Island. Quite recently a few plants were found with a superficial resemblance to *N. mirabilis* Druce, with which *N. phyllamphora* is now merged, but differing from it in important ways, such as the shape of the peristome, the venation of the lamina and the lid, and the number and complexity of the glands under the lid. The Singapore plant cannot be *N. mirabilis*, and since it occurs singly it is probably a hybrid.

Hybrids.

So far as is known, all species of *Nepenthes* can be crossed, producing offspring of great vigour and fertility, which can be used in further crosses; as was done in nineteenth century Europe, where nepenthes breeding had some of the appeal of orchid breeding to-day. Many new varieties were formed; some were beautiful and most sold for high prices. Although gardens hybrids are produced so readily it appears that there is no proved case of a natural hybrid occurring, though taxonomists agree that they probably do. The three possible hybrids in Singapore are *N. hookeriana*, *N. trichocarpa*, and the plant resembling *N. mirabilis*, all of which are rare and generally grow singly. *N. hookeriana* is widely thought to be the hybrid of *N. ampullaria* and *N. rafflesiana*, having some characters of each, and the right geographical and local distribution. The nineteenth century horticulturalists knew *N. hookeriana*, and esteemed it highly; they used it in their crosses, but unfortunately they did not determine its status. *N. trichocarpa* has been accepted as a good species with an odd geographical distribution: Sibolga in N. W. Sumatra, and the Singapore, S. Johore region (Danser, 1928). In the herbarium of the Singapore Botanic Garden however Holttum has classed it as hybrid of *N. ampullaria* and *N. gracilis*, and the appearance of the plant and its occurrence, in Singapore, make this very probable. The third possible hybrid resembles *N. trichocarpa* even more than it resembles *N. mirabilis*; and it is perhaps a cross of *N. trichocarpa* with *N. gracilis*. All of the three possible hybrids are very vigorous and pleasant to cultivate, producing plenty of good-sized pitchers under a fairly wide range of external conditions; unfortunately this is not true of the three good species.

* Present address: c/o Institute of Education, University of Keele, Staffordshire, England.

Distribution of *Nepenthes* species in Singapore. (See Map).

Nepenthes has an ancillary food supply in the prey caught and digested in its pitchers, and it might be expected that it would grow on peculiarly infertile soil. This is indeed so. Singapore soils are of volcanic, sedimentary or alluvial origin, and *Nepenthes* is recorded from the first two of these but not from the richer alluvium. Thus *N. gracilis* is found on the sedimentary outcrop at Ponggol Point, but not further inland, and there are many old records of *Nepenthes* growing on the granite at Changi, but none from the alluvial Tampines region just inland from this. At first sight the Tampines scrubland is very similar to that in which *Nepenthes* grows on volcanic and sedimentary soils, and some of the same plants associated with *Nepenthes* in such sites, can be found there; these include *Melastoma malabathricum* and *Dicranopteris linearis*, which are both abundant. Others however are absent; *Lycopodium cernuum*, a constant associate of *Nepenthes*, is most rare, and *Dillenia suffruticosa* is represented only by occasional unhealthy-looking plants. Evidently the region is unsuitable for *Nepenthes* only in its soil. The Tanah Merah cliff in the alluvial region, which bears *Nepenthes*, appears to be an exception, but in fact it is not so; the *Nepenthes* grow on exposed ancient rock below the alluvial level.

In the sedimentary and volcanic regions all the local *Nepenthes* spp. can be found growing together, though their relative frequencies vary. Typical habitats are:—

1. *Coastal cliffs.* e.g. Tanah Merah, Labrador, Tanjong Gul. Pulau Tekukor.

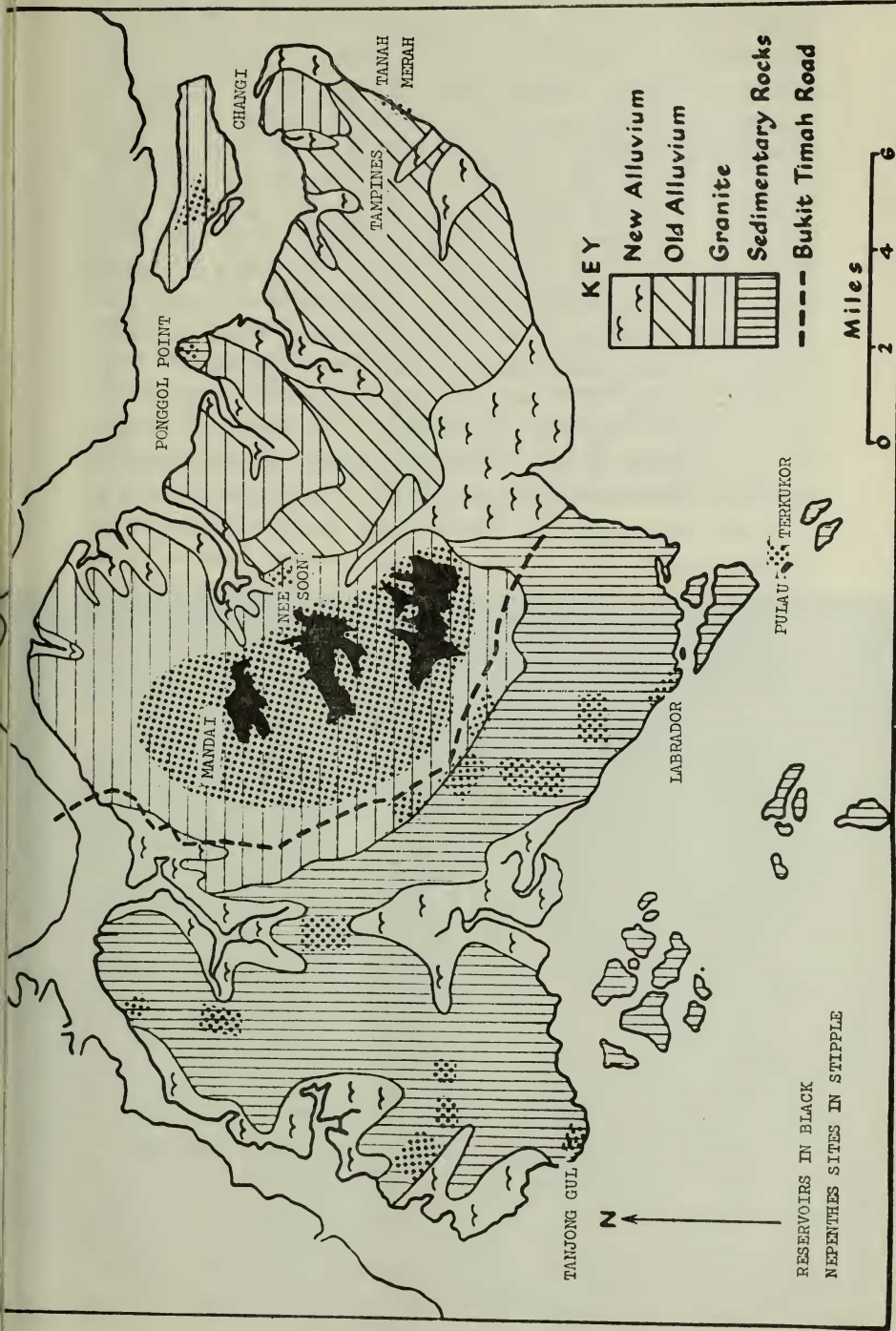
There is no record of clearing or burning of the cliff vegetation, so that it may be primary. The *Nepenthes* found here are often very large indeed, flowering and fruiting abundantly, and with many pitchers. *N. rafflesiana* predominates.

2. *Roadside cuttings.*

This is a habitat resembling the coastal cliffs in many ways, though the cuttings are usually less exposed than the cliffs, and many of them are of course quite recent. The *Nepenthes* are often very numerous, though smaller than the cliff plants. Flowers, fruits and seedlings are numerous. *N. gracilis* predominates.

3. *Regenerating waste ground.*

In Singapore there are many areas which have been cleared, farmed and abandoned after the soil is exhausted. Exposure to high insolation, leaching and erosion lowers the fertility still more. Their history, if they are undisturbed, is of a slow change from sandy wastes to secondary forests; Holttum (1954), Gilliland (1958) and others have recorded the stages. It is not known at what stage in the succession the *Nepenthes* plants first appear, but they are not among the pioneers. In the scrub stage — Holttum's "Adinandra Belukar" — all the local species are common climbing in the bushes. All flower and fruit and there



Distribution of *Nepenthes* on Singapore Island.

are many seedlings. *N. gracilis* predominates. By the time the succession has reached forest conditions the relative frequency of the species has changed; *N. rafflesiana* is now rare, *N. gracilis* is less common and *N. ampullaria* predominates. This is the situation where the forest is comparatively open and the trees of no great height; it can be seen at present around the margins of Pierce and MacRitchie Reservoirs. With the growth of the trees the height of the *Nepenthes* has increased; they can be seen among the branches 30 ft. or more above the ground. Seedling plants, chiefly *N. ampullaria*, can be found, usually along rides where these are lower than the forest level, so that there are sloping banks rather like miniature cliffs on which the small plants grow. In denser forests such as that bordering Mandai Road the relative frequency of the species changes again; here *N. ampullaria* is very plentiful, but the other two species are quite rare. There are no flowers but *N. ampullaria* proliferates from shoots on prostrate stems. Its dense clumps of ground pitchers are extraordinarily numerous, but on the few plants of the other species pitchers are rare. The plants are old; that and the absence of flowers and seeding suggests that they are the last survivors from an earlier stage of regeneration. This is the end of the *Nepenthes* period in the re-development of forest; the plants are absent from well-established secondary forest, as they are from primary Dipterocarp forest.

4. Peat swamp. Nee Soon.

Singapore has one small peat swamp at Nee Soon in which *Nepenthes* is plentiful. All the local species grow on the banks of the broad cutting leading to the swamp, with some hybrids; seedlings, particularly of *N. ampullaria*, are abundant. In the swamp itself there is no *N. ampullaria*; *N. gracilis* is common, small plants apparently growing on detritus floating on the water, and larger ones growing from islands formed round the bases of *Ploiarium* trees, where *N. rafflesiana* is also found. The island plants are in no way stunted — they are in fact very fine. Both species flower and fruit.

It appears that the ecological needs of the three common Singapore species of *Nepenthes* are somewhat different. The sites on the cliffs, cuttings and waste ground can perhaps be considered together as a continuum, with the cliffs at one end of the scale and secondary forest at the other; on such a scale shade, soil water content, fertility and pH increase together, maximum temperature, diurnal temperature range and evaporating capacity of the air decrease; with available water still further reduced on the cliffs by salt spray. From the distribution it is clear that the more exposed, less fertile end of the continuum is best suited to *N. rafflesiana*, the shadier, moister, more fertile end to *N.*

ampullaria; while *N. gracilis* finds optimum conditions between the extremes. The differences are not great; there is, for instance, a very fine female plant of *N. ampullaria* growing on the Tanjong Gul cliff, and fruiting abundantly; however this is an exception, and its seedlings do not survive. The Nee Soon peat swamp ranges from a cutting in secondary forest through increasingly acid, infertile, physiologically dry conditions to the wet centre. The *Nepenthes* distribution follows a predictable pattern, with all species growing in the cutting, *N. ampullaria* predominant at the forest edges, and *N. gracilis* alone with one or two plants of *N. rafflesiana* in the standing water at the centre. Anderson (1963) in a study of the coastal peat swamps of Sarawak records a similar distribution. After zoning the bogs into Phasic Communities 1 — 6, P.C. 6 being the climax, he found *N. ampullaria* occasional in P.C.s 1 and 2, *N. gracilis* frequent in P.C. 4 and surviving though stunted in P.C. 6, and *N. rafflesiana* rare in P.C.s 3 and 4 but frequent in P.C. 6. In peat swamp as well as belukar *N. rafflesiana* favours the most infertile conditions, *N. ampullaria* the least.



Plate 1. *N. ampullaria* Jack.

Ground, stem and leaf pitchers. Water Catchment Nature Reserve, Singapore.

Some Ecological Factors affecting Distribution.

An exhaustive account of the ecology of the local *Nepenthes* cannot be attempted here, but a general description of some of the important points may help in understanding distribution. All the Singapore species grow on the same or very nearly the same sites, only their relative frequency varies; so that their ecological needs can all be considered together. These are met not only in the belukar and cliff habitats, which are clearly rather similar, but also in the peat swamp. In Borneo the same species grow in peat swamps and also in the heath forests, which have some resemblance ecologically to the Singapore belukar. The two kinds of habitats have in common acid, highly infertile soil, which is widely recognised as being a necessity, perhaps the prime edaphic one, for the growth of *Nepenthes*. Indeed in 1914 Barrowcliff proposed using the plants as an index of soil poverty. Macfarlane (1922) thought that a well-aerated soil was also essential, and cultured his plants accordingly; but this can hardly be so for the peat swamp plants, which prosper as well as the belukar ones. Aeration is evidently not important. Available water is low in the peat swamps, the belukar has spells of aridity, and as well, *Nepenthes* is particularly abundant on slopes and cliffs, from which the water drains quickly. Anatomically the plants show signs of xerophytic adaptation, which fit them to survive on a dry soil, though this may not be essential.

Cultivating *Nepenthes*, even in a suitable soil, is somewhat difficult because their growth is much affected by climatic factors. Holttum (1938) pointed out that the micro-climate changes during the upward growth of climbing plants; so that adaptive changes in their responses to external conditions are to be expected. These are not very evident in *Nepenthes* until the flowering stage: although the plants do show very considerable changes in morphology during their growth, their response to climatic factors appears to be relatively constant.

The Seed and Seedling.

About 10,000 seeds are produced from one inflorescence of *N. gracilis*. The seeds are remarkably light, and are winged, so that they can be dispersed by the wind over long distances. Each of the two filamentous wings is hollow, so that the seeds are buoyant; they can be carried for short distances by rainwater rills. Wastage is obviously high by either method of dispersal, but the seeds are so numerous that some must find their way to suitable habitats. Garrard (1955) estimated the viability of *N. gracilis* as 8.3 per cent but counts made by the author gave 79 per cent and 63 per cent; Stern (1917) mentions differences in fertility in seeds from different parts which may account for the discrepancy, and probably viability does not limit distribution. The seeds germinate in the light, and within limits increasing the light shortens the time required. This is a fortnight to three weeks after sowing for most of the seeds, but for others it is very much longer; as late as six or seven months after sowing it is still possible for seeds to

germinate. This variation may have some survival value, since the seedlings emerge into different climatic conditions, some more suitable than others. The seedling is very small. From the first it is adapted to life on infertile soil, since the leaves, though markedly different from those of any adult plant, all bear tiny pitchers. These are functional with digestive glands in the cavities. The attractive glands, which are so numerous and so complex in adult pitchers, are restricted in the primary leaves to the rudimentary rim under the mouth. Development is slow; a tiny rosette of leaves is formed, and the plant remains in this form for the next two or three years, with successive leaves gradually getting larger, and successive pitchers slowly changing towards their adult form. The seedling is quickly killed by dessication, either by wind or by strong sunlight, and this even in damp soil, which perhaps sufficiently explains the absence of *Nepenthes* from the pioneering plants on bare ground. The seedling root is a very meagre one, and often does not appear until after the cotyledons; wind can uproot the small plants, as well as dry them. If the humidity is high the seedlings survive even in a seemingly dry soil, though it is not clear how this is achieved. A bunch of long, tough root hairs appears outside the seed case even before the tip of the root shows, but these are not enough for anchorage and they are doubtfully enough for absorption. Stern (1917) suggested that the seed coat was important, supplying water by capillary action along its furrows. Macfarlane (1908) thought that minute glands scattered all over the surface of the cotyledons and leaves absorbed moisture directly from the air, though not all authors agree with him. The problem is intriguing, but to understand distribution it is perhaps enough to note that the seedlings are adapted for life where the humidity is high, the air is still, there is some shade, and not over-much dependence on soil water. In such situations they are found—at the base of bushes, in nooks on banks and along forest rides. However, there is another limitation; in shade — by no means sufficient to cause etiolation — no pitcher is formed, but only a large lamina. It is unlikely that the seedlings can survive this deprivation for long.

The mature Plant.

The need for humidity, and a rather limited light tolerance, dominate the life of the older plant as they do that of the seedling; though as the plant matures some protective adaptations develop. The cuticle thickens, the young leaf, exposed in the seedling, is shielded in the older plant, the rudiment of the pitcher — the most vulnerable part — is wrapped in hairs. But exposed leaves still curl' pitchers wither, actual burnt patches appear. Nevertheless the plants, once established, survive quite adverse conditions, sometimes even fire. No doubt sheer size plays a part; a patch of strong sunlight kills the whole of a seedling, but only one or two leaves of a large plant. Also the root system becomes extensive, and once the rhizome is formed new growth can come from that. The effect of light can be seen most clearly if the growth of pitchers is watched.

Where shade is too deep pitchers and tendrils do not develop on stem or rosette leaves, laminae become large and thin. If exposure is not high enough for burning, but still too high, both pitchers and their laminae are small; some leaves, notably in *N. rafflesiana*, show twisting of the lamina as well as of the tendril, bringing the pitcher away from exposure. The species all react in this way until climbing is some way advanced; after that there are differences which may be related to their slightly different habitats. Singapore has among its three common species one that is simple, and two that are highly specialised in quite different ways. The simple species, *N. gracilis*, normally has a pitcher on every leaf, borne on the end of a tendril which can coil round supports. The pitchers are tubular and not very large; the wings are never wide, and may be absent. On leaves at the base of the plant, the pitcher mouth opens inwards, towards the stem; on the upper parts it opens outwards. This twisting round of the upper pitchers appears to be normal in the development of *Nepenthes*, since it occurs in most species. In the simpler species, like *N. gracilis*, it is a gradual process with intermediate stages; it involves no change in the shape of the pitcher beyond a slight narrowing of the base, and no change either in the response to light. Matters are quite otherwise with



Plate 2. *N. gracilis* Korth.

Growing on the surface of the freshwater peat swamp forest, Nee Soon area of the Water Catchment Nature Reserve, Singapore.

the more specialised species; not only is the change in direction of the pitcher opening quite sudden, between one leaf and the next, but there may be a dramatic change in the shape of the pitchers. *N. rafflesiana* is such a species. An altogether stouter plant than *N. gracilis*, it has correspondingly larger pitchers. The lower ones are broad-based with widely reaching wings; usually they sit on the ground, joined by straight tendrils to their laminae — which may be two feet or more above their level. The upper pitchers are wingless, with the base so narrowed and curved that they have been described as cornucopias. There are clearly biological advantages in this form; not only is wind resistance lessened, but so also is the volume of digestive fluid in the base which has to be supported, while the trapping area round the mouth remains wide. The two types of pitcher respond differently to light. In conditions of under or over-exposure pitchers or tendrils develop on neither; but where exposure is right, the tendril of the lower pitchers grows rapidly downwards, carrying the pitcher away from the light — which is normally of course towards the base of the plant. The tendril of the upper pitchers grows outwards in an arc, and normally coils round a support before the pitcher grows too big for this to be possible. The lower pitchers wither very easily; they cannot survive even that amount of exposure which, when applied to the lamina, stimulated their development. The upper pitchers are



Plate 3. *N. rafflesiana* Jack.
On the sea cliffs of Pulau Tekukor, Singapore.

more resistant, though still less hardy than their laminas. The upper and lower leaves are adapted to different conditions in fact; as much in their tropistic responses as in the different shape and hardness of their pitchers. Evidently making the best of two worlds is a feature of *Nepenthes* organisation; *N. rafflesiana* — and most other species too — can catch not only running insects on the ground, but — with the mouths of the upper pitchers opening invitingly outwards — flying insects as well, though the catch of flying insects is in fact small. *N. ampullaria* is specialised in a different fashion; each

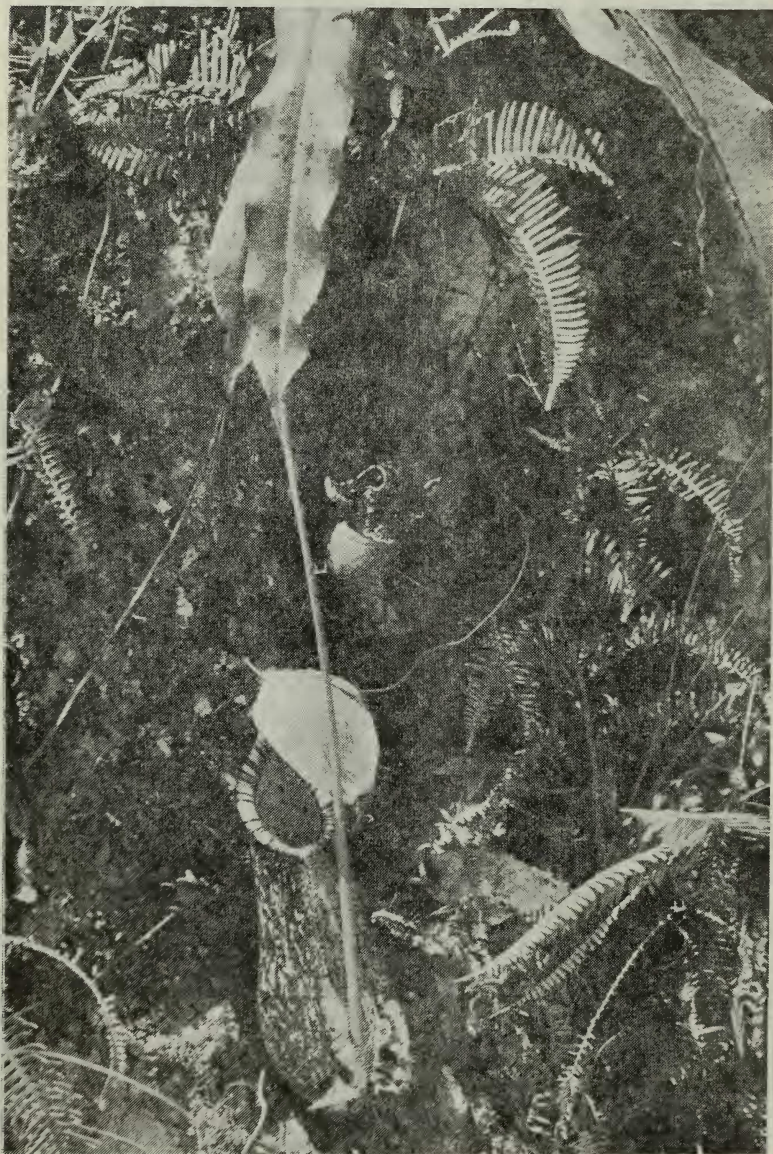


Plate 4. *N. rafflesiana* Jack.
Ground Pitcher.

leaf on the lower part of the growing stem bears a pitcher on a short tendril which does not coil, but on the upper leaves, although there is a coiling tendril, the pitcher does not develop. There is no record of a pitcher of *N. ampullaria* in which the mouth opens outwards. As the lower leaves and their pitchers die, they are not replaced. Instead ground pitchers appear at the base of the plants, borne on short shoots from prostrate stems and rhizomes. Each shoot bears a tight rosette of pitchers, in which the rudimentary laminas and tendrils serve only to bring the pitchers into position. In forest conditions the ground pitchers cover large areas of forest floor, half hidden in fallen leaves; they must be a most efficient trap. Similar pitchers can appear on the brown, seemingly lifeless stems that climb high in the trees. In effect, *N. ampullaria* bears two kinds of leaves, one photosynthetic and climbing, the other absorbtive, Perhaps this is a biological advantage, since its distribution is wider than that of the other local species, not only locally but geographically, and it can grow at higher altitudes. The ground pitchers are borne in quite dense shade, which is sometimes provided on open ground by the bushy growth of this remarkably adaptable plant. Many species of *Nepenthes*, including all the Singapore ones except *N. rafflesiana*, can produce clumps of ground pitchers from the mature plants. The pitchers have the same form as those from the leaves on the lower part of the stem; as in *N. ampullaria* their laminas and tendrils are so reduced as to be scarcely discernible. These ground pitchers are a remarkable development; all other leaves of the plants show enlarged laminas when they are grown in shade, and pitchers are not produced.

Cultivators of *Nepenthes* in private or botanic gardens are sometimes troubled by a scarcity of pitchers. This can be due, not only to too much or too little shade, but also to too rich a soil (Smythies 1963). Such pitcherless plants sometimes flower and seed normally. Evidently carnivory is not obligatory, at least for older plants, though it may well be for early stages, since *Nepenthes*, growing naturally, is usually excluded from habitats with rich soils.

The Flower

The inflorescences are terminal, though growth continues from lateral shoots. The climbing habit has the effect of bringing the flowers out into the open, to the advantage of both pollination and seed dispersal. They appear only where they can be fully exposed, so that they protrude from the tops and sides of trees, and a foot or more over the tops of bushes; and it seems that no degree of exposure can be too high. A different micro-climate indeed from that of preceding stages! A few leaves project along with the inflorescences, and these are pitcherless — according to Stern, because of diversion of food to the inflorescence. But this is to neglect the function of the pitchers in procuring food, and it

is perhaps more probable that the pitchers fail through over-exposure. Few flowers remain unfertilised, but it is uncertain how fertilisation is accomplished. The surfaces of the tepals are dotted with large glands, which secrete so much nectar that it fills the base of the spoonshaped tepals; nevertheless the flowers are seldom visited by insects, not even by ants. Because of the dioecious habit, and the floral structure, a pollinating insect would need to be large and winged. The writer once had the good fortune to watch a bee absorbed in drinking the nectar, which it did while straddling the stamen column with its body. Such insects are well-fitted to be pollinators, but there is no other report of their visiting the flowers. Pollination is probably mainly by wind. Dr. Pallot, lately of the Botany Department, University of Singapore, points out that the pollen grains, though joined together in tetrads, are small enough for this to be possible.

Conclusion.

Nepenthes distribution in Singapore appears to be rather narrowly limited to the most infertile areas which can also provide suitable climatic conditions. The plants are in fact fairly widespread, but this reflects rather the prevalence of man-made waste ground than any abundance of natural sites, of which only the cliffs and perhaps Nee Soon swamp give any picture. The *Nepenthes* population must have been quite small before cultivation began on Singapore Island; and must become so again as one site after another is taken over for industrial and other development.

All things considered, it cannot be said that *Nepenthes* is ideally adapted to the dryland conditions in which it grows in Singapore, especially in the early stages. The leisurely growth, the meagre root, and the readiness with which the small plants — and the older pitchers — dry out, all suggest an origin in a different habitat. It is tempting to see this in the peat swamps, home of many insectivorous plants; and to suggest that the ancestral *Nepenthes* invaded the dry land where it found a suitable soil and tolerable climate. However, for the Singapore species in the existing lowland swamps in Sarawak light is insufficient; Anderson describes them as appearing to climb only where there is an opening in the tree canopy, and only the climbing plants can reproduce. The ancestral home of *Nepenthes*, as so much else concerning these unusual plants, must remain problematic.

Acknowledgements

I have to thank the late Professor H. B. Gilliland, of the University of Singapore, Mr. B. S. Smythies and Dr. J. A. R. Anderson, both of the Forestry Department, Sarawak, and Mr. H. M. Burkill, Director of Singapore Botanic Gardens, for their help, and my husband, for the photographs.

REFERENCES

ANDERSON, J. A. R. The Flora of the Peat Swamp Forests of Sarawak and Brunei.

Gard. Bull., Sing. 20, 2. 1963.

BARROWCLIFF, M. Malayan Rubber and Coconut Soils.

Trans 3rd. Internat. Cong. Trop. Agric. 2, 1914.

DANSER, B. H. The *Nepenthaceae* of the Netherlands Indies.

Bull. Jard. bot. Buit. ser. 3, 9, 1928.

GARRARD, A. The Germination and Longevity of Seeds in an equatorial Climate.

Gard. Bull., Sing. 14, 2. 1955.

GILLILAND, H.B. Plant Communities on Singapore Island.

Gard. Bull., Sing. 17, 1958.

HOLTTUM, R.E. *Adinandra Belukar*. A succession of Vegetation from bare ground on Singapore Island.

Mal. Journ. Trop. Geog. 3. 1954.

HOLTTUM, R. E. (through Richards) The Ecology of Tropical Pteridophytes in Verdoorn's *Manual of Pteridology*. The Hague 1938.

MACFARLANE, J. M. *Nepenthaceae. Das Pflanzenreich*. Leipzig 1908.

MACFARLANE, J. M. *Nepenthaceae. Standard Cyclop. Hort.* New Ed. 4 1922.

RICHARDS P. W. *The Tropical Rain Forest*. O.U.P. 1952.

STERN, K. Beitrage zur Kenntnis der Nepenthaceen. *Flora*, 109. 1917.

SMYTHIES, B. E. *The Distribution and Ecology of Pitcher-plants (Nepenthes) in Sarawak*. Symposium on Ecological Research in Humid Tropics Vegetation, Kuching, Sarawak, July 1963. UNESCO Science Co-operation office for South-east Asia, 1965.